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Are *Monobia* and *Montezumia* Monophyletic? A Cladistic Analysis of Their Species Groups Based on Morphological Data (Hymenoptera, Vespidae, Eumeninae)

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ABSTRACT

A concept of the higher-level phylogeny of the Eumeninae remains elusive. As such, the naturalness of several genera occurring in the Neotropical region is doubtful, including *Monobia* and *Montezumia*. Morphological data were used to infer the phylogenetic relationships among the species groups within both genera, as well as to test their monophyly. Analyses recovered *Monobia* and *Montezumia* as monophyletic as long as *Montezumia arizonensis* and *Montezumia aurata* were included in *Monobia*. Most species groups proposed by Willink in 1982 were also recovered as monophyletic. Three new combinations are proposed in congruence with the phylogenetic results: *Monobia arizonensis,* new combination, *Monobia aurata,* revised combination, and *Monobia oaxaca,* new combination. An additional new species is described: *Monobia goiana* Hermes, new species.

KEY WORDS: cladistics, Eumeninae, Neotropical, phylogeny, wasps.

INTRODUCTION

There are 53 genera and about 1050 species of Eumeninae occurring in the New World (Carpenter and Garcete-Barrett, 2003 [2002]; Carpenter, 2004; West-Eberhard et al., 2006). The

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fauna of this region has received little attention regarding its suprageneric and generic classification, especially in the Neotropics. During the last century, the splitting of old Eumeninae genera into several others, as well as proposals for new ones, were undertaken by many authors (Bohart, 1940; Parker, 1966; Willink, 1967; Snelling, 1975; Giordani Soika, 1978; Bohart, 1982; 1984; Giordani Soika, 1990), resulting in generic classifications that must be rationalized by the synonymy of numerous taxa (Carpenter and Garcete-Barrett, 2003 [2002]). Furthermore, the current classification was never tested by cladistic methods, which reinforces the opinion that irrational splitting might have resulted in the creation of unnatural taxa.

Monobia de Saussure and *Montezumia* de Saussure are two Eumeninae genera ranging from the United States to northern Argentina, with the high peak of its diversity occurring in the Neotropics. Thirty-one and 48 species are described for *Monobia* and *Montezumia,* respectively. Although both taxa are from a region in which taxonomic practices were based on splitting rather than lumping, they are not the result of the splitting of one genus: both were described in 1852 by Henri de Saussure in his monograph on the *Tribu des Euméniens,* each comprising a reasonable number of new species descriptions as well.

In 1875 de Saussure, in his synopsis of the American wasps, compared *Montezumia* to *Monobia,* mainly because of the identical number of labial and maxillary palpomeres. He tried to separate them using the form of the first metasomal segment as a diagnostic character, but made clear that transitory forms always occurred. De Saussure (1875) divided *Montezumia* into five divisions, while two other divisions were delimited within *Monobia.* Zavattari (1912) was the first author to comprehensively revise both taxa. He recognized 27 species for *Montezumia* and 21 for *Monobia,* and also created the genus *Pinta* for the species *chalybea* de Saussure, previously placed in the division *Antezumia* of *Montezumia.* Also, Zavattari restricted both genera to include only American elements.

Bequaert (1921) published a synopsis of the genus *Montezumia,* dividing it into four divisions: *Montezumia, Antezumia, Pseudozumia,* and *Acarozumia. Antezumia* is currently recognized as a monotypic Neotropical genus and is a senior synonym of *Pinta* Zavattari. *Pseudozumia* is currently composed of six valid species that occur in the Afrotropical and Oriental regions. The remaining species recognized by Bequaert (1921) within *Pseudozumia* are placed in other genera, which occur in the Afrotropical and Oriental regions. Finally, *Acarozumia* is composed of three species occurring in the Australian and Oriental regions. Like de Saussure (1875), Bequaert (1921) stated that the differences between *Montezumia* and *Monobia* were arbitrary. The recognition of *Montezumia* as currently known (i.e., containing only American elements) was also followed by Bequaert (1940a; in agreement with Zavattari's [1912] concept).

Later, Bequaert (1940b) published a synopsis of the genus *Monobia* wherein he recognized 21 structural forms plus five color forms (varieties). Once again, he noted that difficulties may arise when trying to hold *Montezumia* and *Monobia* as separate taxa, as follows: "No definite limits can be drawn between *Montezumia* and *Monobia,* although the typical members of each genus are readily placed. For this reason I have included in my key the North American *Montezumia arizonensis* J. Bequaert, which may well be sought under *Monobia* and is very similar in coloration to *Monobia texana.*"

The most recent revision of both *Monobia* and *Montezumia* was published by Willink (1982), who presented a series of characters to distinguish the two genera. Although many species are readily placed, the presence of many transitory forms was noted once again, making the diagnosis of both taxa subjective. Moreover, Willink (1982) considered that *Monobia aurata* Bertoni belongs to *Montezumia,* remarking that most of the characters presented by this species made it fit better within the *Montezumia.* Another taxonomic procedure adopted by Willink (1982) was the elimination of all divisions within each genus, recognizing only species groups. Although arbitrariness concerning the limits of *Monobia* and *Montezumia* remains, the monograph presented by Willink (1982) is by far the most comprehensive one, with a complete taxonomic background, descriptions of several new species, illustrations, distributional maps, and keys to species level.

Carpenter and Cumming (1985) investigated the relationships among the Nearctic genera of Eumeninae, with *Montezumia* and *Monobia* recovered as sister groups placed in their *Montezumia-Pseudodynerus* component, which was supported by the slitlike form of the axillary fossa. All other genera included in this component were recently studied: *Pseudodynerus* de Saussure had its species relationships investigated by Hermes and Melo (2008) and Hermes (2010); *Paranortonia* (now *Parazumia* de Saussure) was revised by Carpenter and Garcete-Barrett (2005); another related genus, *Plagiolabra* von Schulthess, not included in Carpenter and Cumming's (1985) analysis as it is Neotropical, was also corroborated as monophyletic by Hermes and Melo (2008). The case of *Montezumia* and *Monobia,* however, requires further investigation.

In the present work, the naturalness of *Monobia* and *Montezumia* were put to the test by using morphological evidence to reconstruct the phylogenetic relationships within the clade *Monobia-Montezumia.* Furthermore, the monophyly of the species groups proposed by Willink (1982) was also investigated. Three new combinations and one new species are proposed.

MATERIALS AND METHODS

The Study of Morphology

Material from the following institutions was examined: American Museum of Natural History (New York), Coleção de Entomologia Pe. Jesus Santiago Moure, Universidade Federal do Paraná (Curitiba, Brazil), and Museo Nacional de Historia Natural del Paraguay (San Lorenzo, Paraguay).

The study of the external morphology was carried out through examination of dry, pinned specimens. Both adult females and males (when available) were examined for character circumscription. Male genitalia were also studied. The genital capsules were detached from the metasoma, heated and cleared in lactophenol, and stored in glycerin. Structures were observed under a stereoscopic microscope ZEISS Stemi SV6. Photographs of relevant structures were obtained with a Leica DFC 500 digital camera attached to the stereoscopic microscope Leica MZ 16. The images were captured with the software IM 50 (Image Manager) and mounted with the software Auto-Montage Pro 5.03.0040.

TABLE 1. Number of terminals used for each species-group within *Monobia* and *Montezumia* following the classification proposed by Willink (1982)

Species group	Species (*N*)	Total species (*N*)
Monobia caridei	1	2
Monobia angulosa	12	29
Montezumia arizonensis	1	2
Montezumia azurescens	3	7
Montezumia ferruginea	1	1
Montezumia leprieurii	3	11
Montezumia nigriceps	4	7
Montezumia dimidiata	3	6
Montezumia infernalis	4	14

Taxon Sampling

In order to test the monophyly of *Monobia* and *Montezumia,* species representing all species groups proposed by Willink (1982) were included (table 1). A total of 32 species belonging to either *Monobia* or *Montezumia* were used as ingroup taxa. As outgroup taxa, species in the genera *Parazumia, Plagiolabra, Pseudodynerus,* and *Stenonartonia* were included. Character polarization was obtained posterior to the analyses by rooting (Nixon and Carpenter, 1993). Trees were rooted between *Stenonartonia apicipennis* (Fox) and the remaining taxa. Abbreviations for *Monobia* and *Montezumia* are *Mb.* and *Mt.,* respectively, to allow ready distinction between species included in each genus.

Cladistic Analyses

Characters were treated as nonadditive (Fitch, 1971). The matrix was constructed in Winclada (Nixon 2002), and the searches for most-parsimonious cladograms performed with the software TNT 1.1 (Goloboff et al., 2008a). Characters were treated using equal weights and implied weights (Goloboff, 1993). Under implied weights, values of the constant *k* between 3 and 10 were tested. The New Technology Search protocols were used for both character weighting schemes, with the algorithms Ratchet (Nixon, 1999; Perturbation Phase adjusted to 25 and 5 for upweighting and downweighting respectively, plus 200 iterations), Drift (Goloboff, 1999; 20 cycles), and Tree Fusing (Goloboff, 1999; 100 rounds) implemented. Each round of analysis comprising the full set of algorithms was performed until minimum tree length was hit at least 100 times. Clade support was investigated through the symmetric resampling method (10,000 replications) (Goloboff et al., 2003) and Bremer support (Bremer, 1994) (suboptimal trees up to 15 steps longer), also performed in TNT 1.1.

RESULTS AND DISCUSSION

Cladistic Analyses

A total of 49 characters were circumscribed after examination of the specimens (tables 2 and 4). Thirty-nine characters were derived from external morphology, while 10 were limited to male genitalia.

TABLE 2. Character list for *Monobia* and *Montezumia*.
Characters were extracted from females except where explicitly indicated

1. Number of maxillary palpomeres: (0) six; (1) five.
2. Number of labial palpomeres: (0) four; (1) three.
3. Inner axis of mandibles: (0) toothed; (1) not toothed.
4. Apex of labrum: (0) longer than wide; (1) wider than long.
5. Apex of clypeus: (0) slightly concave (fig. 5); (1) deeply concave (fig. 6); (2) truncate (figs. 7–9).
6. Clypeal dimensions: (0) wider than long; (1) as wide as long; (2) longer than wide.
7. Placement of cephalic foveae: (0) in a slightly raised region on vertex; (1) in a depressed region on vertex (figs. 10–13).
8. Cephalic foveae: (0) margined posteriorly by a carina (fig. 12); (1) not margined posteriorly by a carina (fig. 13).
9. Cephalic foveae: (0) placed halfway between lateral ocelli and occipital carina; (1) closer to occipital carina.
10. Setae on cephalic foveae: (0) dense and long; (1) somewhat sparse, short.
11. Occipital carina, dorsal portion: (0) absent; (1) present.
12. Occipital carina, ventral portion: (0) regular; (1) forked near mandibles.
13. Male antennal apex: (0) rolled backwards and concealed in a cavity on flagellomere VI; (1) not concealed.
14. Inner surface of male flagellomeres IX, X, and XI: (0) with tyloids; (1) without tyloids.
15. Pronotal carina, dorsal portion: (0) absent; (1) present.
16. Height of pronotal carina, dorsal portion: (0) slightly raised, less than half median ocelli diameter (fig. 14); (1) evidently raised, at least reaching half of median ocelli diameter (fig. 15). Applicable only to terminals that received state 1 for character 15.
17. Lateral surface of pronotum: (0) strongly depressed (fig. 18); (1) slightly depressed, almost seeming flat (figs. 16–17).
18. Humeral carina: (0) absent (fig. 16); (1) present (fig. 18).
19. Pretegular carina: (0) present; (1) absent.
20. Mesoscutum, posterior portion: (0) only slightly depressed posteriorly (fig. 20); (1) with evident notauli (fig. 19); (2) with shallow to obsolete notauli (figs. 21–22).
21. Mesepisternum: (0) without carina below pronotal lobe; (1) with carina below pronotal lobe.
22. Epicnemial carina: (0) absent; (1) present.
23. Apical lobe of tegula: (0) truncate (fig. 19); (1) pointed (figs. 20–22).
24. Prestigma: (0) longer than pterostigma; (1) longer than half of pterostigma; (2) less than half of pterostigma.
25. Apical forewing coloration: (0) whitish; (1) as in the remainder of the wing.
26. Metanotum: (0) with lateral longitudinal carina (fig. 25); (1) without lateral longitudinal carina (fig. 26).
27. Metanotum sculpture: (0) space between punctures not raised; (1) space between punctures slightly raised, forming a weak transverse crest (fig. 23); (2) space between punctures strongly raised, forming a strong transverse crest (fig. 24).
28. Dorsal surface of propodeum: (0) at same level as metanotum; (1) below level of metanotum.
29. Posterior surface of propodeum: (0) lamellate on upper portion; (1) not lamellate on upper portion.
30. Posterolateral angles of propodeum: (0) rounded (fig. 26); (1) projecting (fig. 25).
31. Median concavity of posterior surface of propodeum: (0) wide (fig. 25); (1) narrow (fig. 26).
32. Submarginal carina: (0) not raised; (1) slightly raised (fig. 27); (2) strongly raised (fig. 28).
33. Metasomal tergum 1 profile: (0) angular between anterior and dorsal surfaces (fig. 29); (1) not angular between anterior and dorsal surfaces (fig. 30).
34. Metasomal tergum 1 dorsal view: (0) without preapical longitudinal furrow; (1) with preapical longitudinal furrow.
35. Metasomal tergum 1 pre-apical furrow: (0) shallow to obsolete; (1) evident. Applicable only to terminals that received state 1 to character 34.
36. Metasomal sternum 1: (0) less than 3 times as wide as long (fig. 32); (1) more than 3 times as wide as long (fig. 31).
37. Metasomal sternum 1: (0) with carina basally (fig. 31); (1) without carina basally (fig. 32).
38. Base of metasomal sternum 2: (0) without transverse furrow; (1) with transverse furrow.
39. Base of metasomal sternum 2: (0) without lateral humps; (1) with lateral humps.
40. Apex of digitus: (0) rounded (fig. 36); (1) cylindrical (figs. 33 and 35); (2) truncate (fig. 34); (3) slender.
41. Setae on digitus: (0) sparsely setose; (1) densely setose, setae concentrated on apico-dorsal portion; (2) densely setose, setae distributed uniformly.
42. Basal dorsal angle of digitus: (0) acute (figs. 34 and 41); (1) straight to obtuse (figs. 33 and 41).
43. Basal ventral angle of digitus: (0) acute (figs. 34 and 41); (1) straight to obtuse (figs. 33 and 41).
44. Dorsal margin of digitus: (0) without spurs; (1) with spurs.
45. Base of cuspis: (0) with long differentiated setae; (1) without differentiated setae.
46. Basal margin of cuspis: (0) not projected; (1) projected.
47. Aedeagus: (0) ventrally expanded (figs. 37 and 39–40); (1) not ventrally expanded (fig. 38).
48. Ventral lobe of aedeagus: (0) with one evident projection (figs. 38–39); (1) with two spiny projections deeply concave in between (fig. 40); (2) with two weak projections slightly concave in between (fig. 37); (3) with weak angle.
49. Ventral margin of aedeagus: (0) serrate medially; (1) not serrate medially.

TABLE 3. Number of trees recovered under different weighting of the characters.
Abbreviations used: CI = consistency index; RI = retention index

Weighting scheme	Constant *k*	Trees recovered (*N*)	Steps (*N*)	CI	RI
Equal	–	35	149	40	74
Implied	3	9	154	38	73
Implied	4	3	152	39	73
Implied	5	3	152	39	73
Implied	6	3	152	39	73
Implied	7	1	150	40	74
Implied	8	1	149	40	74
Implied	9	1	149	40	74
Implied	10	1	149	40	74

The analysis of the matrix using equal weights returned 35 trees of 149 steps, with the strict consensus shown in figure 1. The analyses using implied weighting and different constant *k* values returned different topologies and number of trees compared to equal weights (figs. 2–4; table 3). We base our discussion on the cladograms using equal weighting and implied weighting under the values 3 (strict consensus tree shown in fig. 2), 7 (single tree shown in fig. 3), and 8 (single tree shown in fig. 4) of the constant *k,* because they differ in terms of the internal relationships among species groups within *Monobia* and *Montezumia.*

The higher-level phylogenetic relationships among eumenine genera remain elusive, with only one published effort including *Monobia* and *Montezumia* as ingroup taxa (Carpenter and Cumming, 1985). Although their results indicate a sister-group relationship between *Parazumia* (formerly *Paranortonia*) and *Monobia* + *Montezumia,* related genera such as *Plagiolabra* and *Stenonartonia* were not included, rendering any topology obtained within this clade inconclusive with regard to a complete sample of relevant taxa. Therefore, we will defer discussion on the relationships of the outgroup taxa.

Both *Monobia* and *Montezumia* were recovered as monophyla, but only if *Montezumia arizonensis* Bequaert and *Montezumia aurata* Bertoni are included in *Monobia* (figs. 1–4). In all analyses, three synapomorphies always supported the clade *Monobia* + *Montezumia*: maxillary palpi with five palpomeres (char. 1, state 1), labial palpi with three palpomeres (char. 2, state 1), and epicnemial carina present (char. 22, state 1) (table 4). This palpal formula is clearly synapomorphic for *Monobia* + *Montezumia* for the major clade in which these genera are placed (Carpenter and Cumming, 1985), and it is a condition considered diagnostic by Willink (1982). The presence of epicnemial carina, however, is also observed in the species of other related genera such as *Pseudodynerus* (e.g., *P. auratoides* Bertoni and *P. carpenteri* Hermes and Melo; Hermes and Melo, 2008) and *Stenonartonia* (the species in the species group of *S. occipitalis* Garcete-Barrett, 2011). One homoplastic transformation also supports *Monobia* + *Montezumia* in every analysis, the cephalic foveae placed closer to the occipital carina than to the ocelli (char. 9, state 1), a condition also shared with *Plagiolabra*. When it comes to the equal-weighting analysis alone, the apex of digitus rounded in the male genitalia (char. 40, state 0) is also synapomorphic for this clade, with several homoplastic changes occurring among lineages
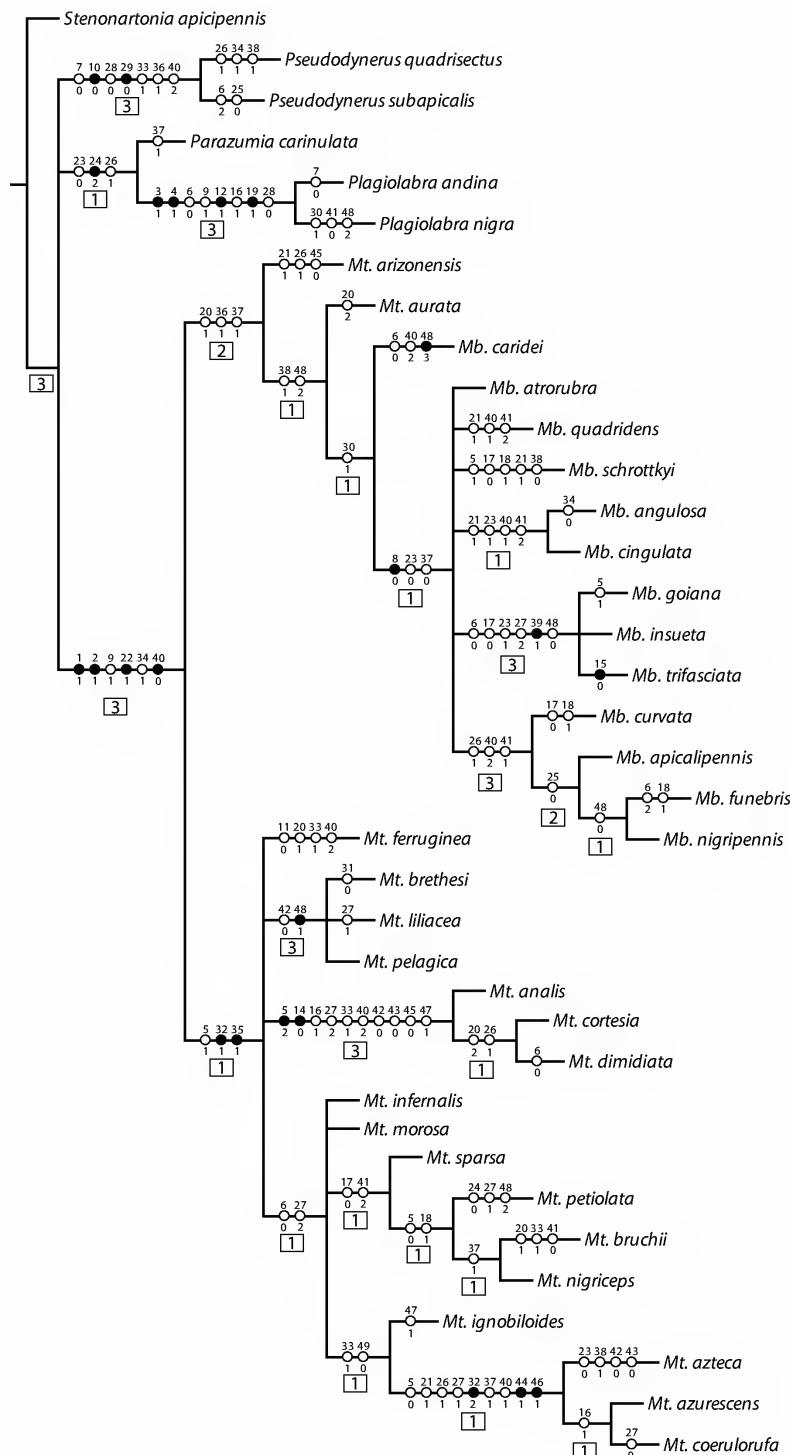
FIGURE 1. Strict consensus cladogram of 35 most parsimonious trees using equal weights of the characters. Black circles indicate synapomorphies and white circles homoplastic changes. *Mb. = Monobia, Mt. = Montezumia*. Bremer support values in boxes below branches. Species group as in figure 2.
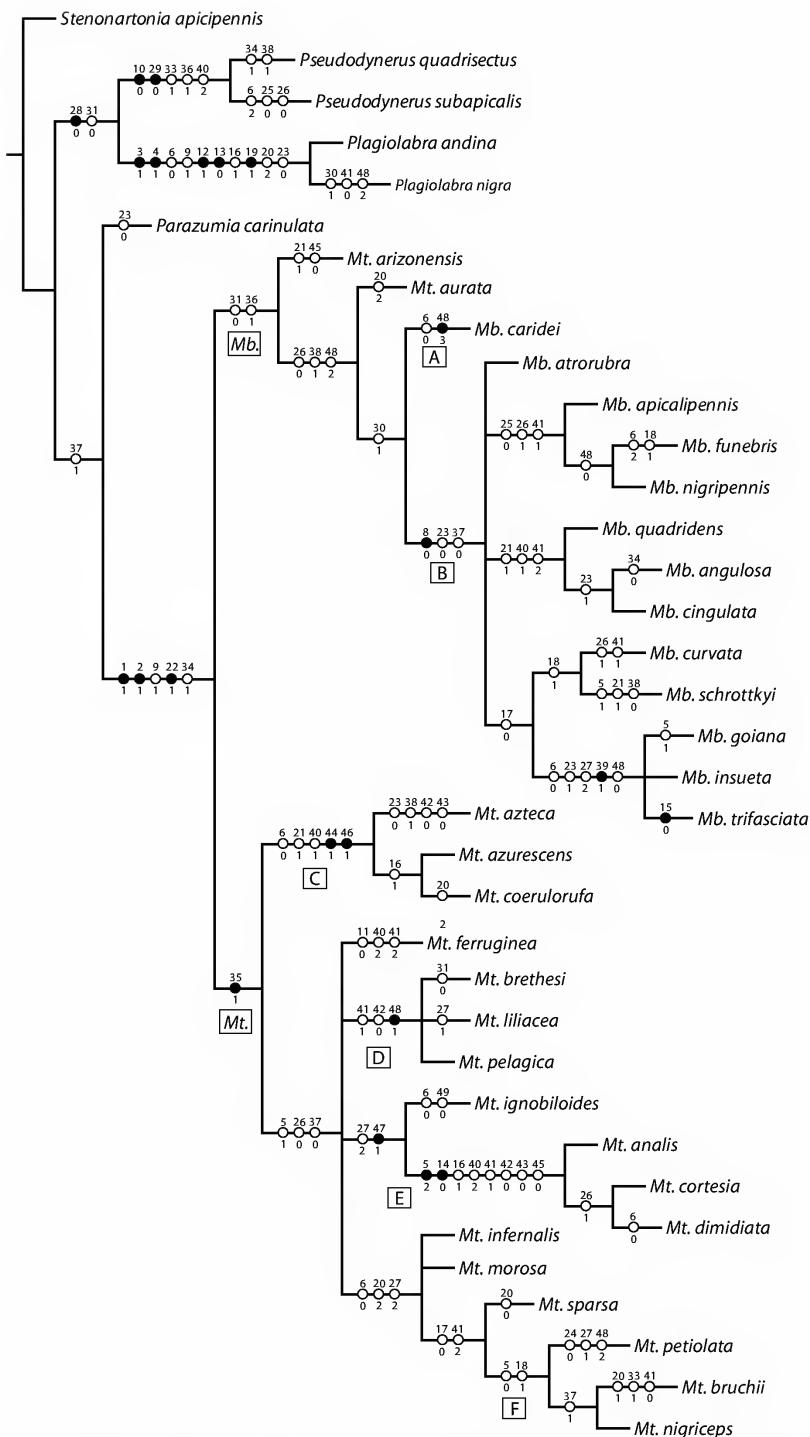
FIGURE 2. Strict consensus cladogram of nine most parsimonious trees using implied weighting of the characters (*k* = 3). Black circles indicate synapomorphies and white circles homoplastic changes. *Mb.* = *Monobia, Mt.* = *Montezumia,* A = *Mb. caridei* group, B = *Mb. angulosa* group, C = *Mt. azurescens* group, D = *Mt. leprieurii* group, E = *Mt. dimidiata* group, F = *Mt. nigriceps* group.
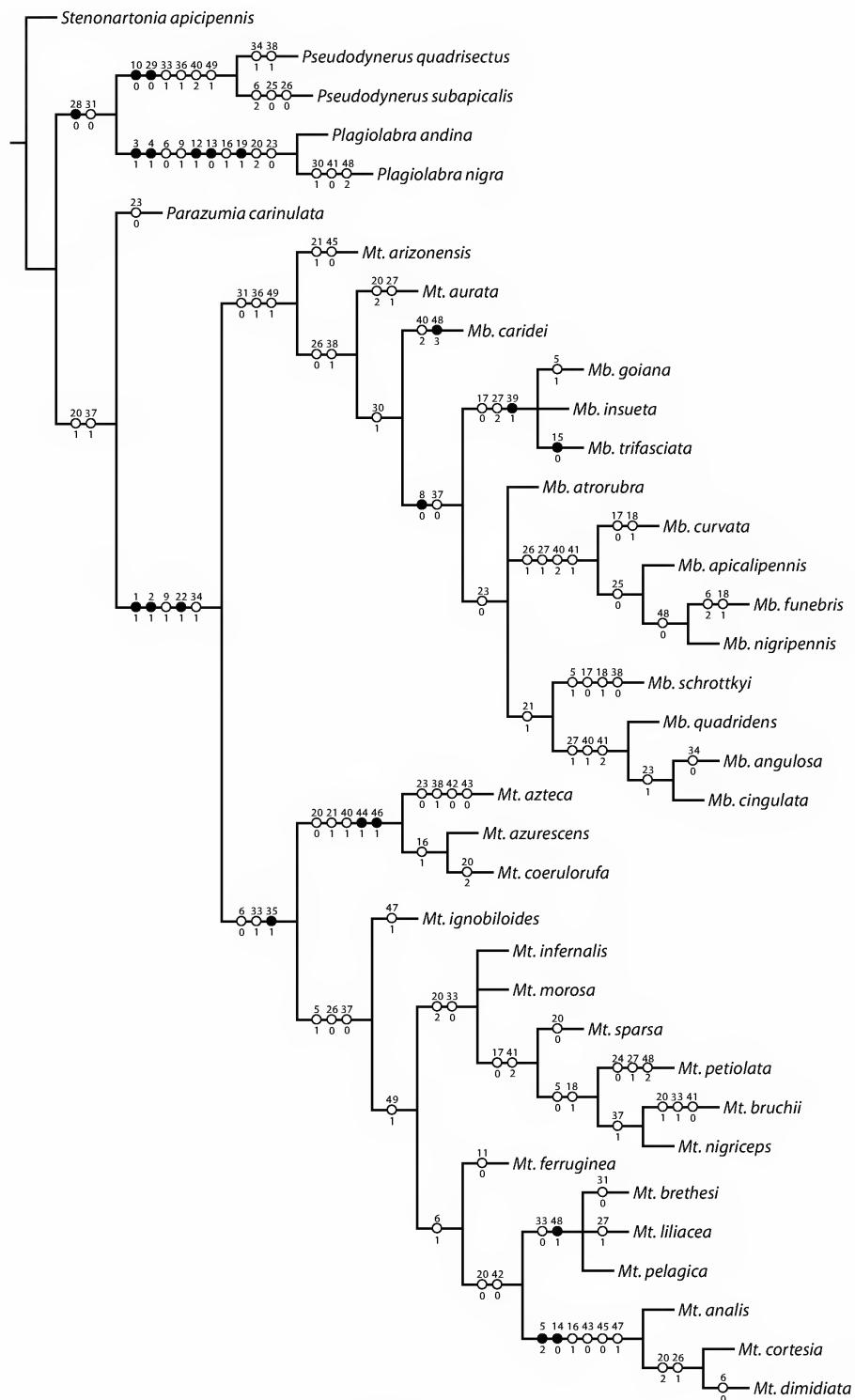
FIGURE 3. Single cladogram obtained with implied weighting of the characters ($k = 7$). Black circles indicate synapomorphies and white circles homoplastic changes.

FIGURE 4. Single cladogram obtained with implied weighting of the characters (k = 8). Black circles indicate synapomorphies and white circles homoplastic changes.

TABLE 4. Character matrix for *Monobia* and *Montezumia* as constructed from morphological data. Symbols used: unseen (?); inapplicable (−)

Characters

Terminals	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Stenonartonia apicipennis	0	0	0	0	0	0	1	1	1	0	1	0	0	1	1	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	−	0	0	0	0	3	2	1	1	1	0	1	0	0	0
Parazumia carinulata	0	0	0	0	0	1	1	1	0	1	0	1	?	1	1	0	1	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	1	−	0	1	0	0	?	?	?	?	?	?	?	?	?	?
Plagiolabra andina	0	0	1	1	0	0	0	1	0	1	1	1	1	0	1	1	1	0	0	2	0	0	0	2	1	1	0	0	0	0	0	0	0	0	−	0	0	0	0	3	2	1	1	1	0	0	0	0	0
Plagiolabra nigra	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	1	1	0	0	2	0	0	0	2	1	1	0	0	0	0	0	0	0	0	−	0	0	0	0	3	0	1	1	1	0	0	0	2	0
Pseudodynerus quadrisectus	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0	1	1	0	0	1	0	1	0	1	0	1	0	0	1	0	1	0	2	2	1	1	1	0	0	0	0	1
Pseudodynerus subapicalis	0	0	0	0	0	2	0	1	0	0	1	0	1	0	1	1	0	1	0	0	0	0	1	1	0	0	1	0	1	0	1	0	1	0	−	1	0	0	0	2	2	1	1	1	0	0	0	0	1
Monobia angulosa	1	1	0	0	0	1	1	1	0	1	1	0	1	1	1	0	1	1	0	0	1	1	0	0	1	1	0	1	1	1	0	0	0	0	−	1	0	0	0	2	1	2	1	1	0	0	0	2	1
Monobia apicalipennis	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	1	2	1	1	1	0	0	0	2	1
Monobia atrorubra	1	1	0	0	0	1	1	1	0	1	1	0	0	1	1	1	0	1	0	0	1	0	1	0	0	1	0	1	1	1	0	0	0	0	−	1	0	0	0	?	?	?	?	?	?	?	?	2	?
Monobia caridei	1	1	0	0	0	0	0	1	0	1	1	1	0	1	1	1	0	1	0	0	1	1	0	0	0	1	0	1	1	0	0	1	0	0	1	0	1	1	0	2	0	1	1	1	0	1	0	3	1
Monobia cingulata	1	1	0	0	0	1	1	1	0	1	1	0	1	1	1	1	0	1	0	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	1	−	1	2	1	1	0	0	0	2	1
Monobia curvata	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	2	1	2	1	1	1	0	0	0	2	0
Monobia funebris	1	1	0	0	0	2	0	1	0	1	1	0	1	0	1	1	0	1	0	1	0	1	0	0	0	2	0	1	1	0	0	0	0	0	1	0	1	0	2	1	1	1	1	1	0	0	0	0	1
Monobia goiana	1	1	0	0	1	0	1	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	1
Monobia insueta	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	1	0	0	1	1	0	0	0	2	0	1	1	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	1
Monobia nigripennis	1	1	0	0	0	1	1	1	0	1	1	0	1	1	1	1	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	1	0	1	0	2	1	1	1	1	1	0	0	0	0	1
Monobia quadridens	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	2	1	2	1	1	1	0	0	0	2	1
Monobia schrottkyi	1	1	0	0	1	1	2	1	0	1	1	0	1	0	1	1	0	0	0	1	0	1	0	0	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	0	1	1	1	1	0	0	0	2	1
Monobia trifasciata	1	1	0	0	0	0	0	1	0	1	1	0	1	1	0	1	0	−	0	0	0	0	1	0	0	2	0	1	1	0	0	0	0	0	1	0	1	1	0	0	0	1	1	1	0	0	0	0	1
Montezumia analis	1	1	0	0	2	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	1	1	1	2	1	1	1	1	1	1	0	0	0	1	0	0	0	2	1	0	1	0	0	0	0	0	1	0
Montezumia arizonensis	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	1
Montezumia aurata	1	1	0	0	0	0	0	1	0	1	1	0	1	0	1	1	0	1	0	2	0	1	0	0	1	1	0	1	1	1	1	0	0	0	0	1	1	0	0	2	0	1	0	0	0	0	0	2	1
Montezumia azteca	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	1	0	1	1	0	1	1	0	0	0	0	1	0	0	1	1	0	0	0
Montezumia azurescens	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	0	1	0	0	1	1	2	1	1	0	0	1	0	0	0	0	1	0	1	1	1	1	1	0	0	0
Montezumia brethesi	1	1	0	0	0	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	1
Montezumia bruchii	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	0	0	1	0	1	0	2	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
Montezumia coerulorufa	1	1	0	0	2	1	1	1	0	1	1	0	1	1	1	1	0	1	0	2	1	1	1	1	1	2	0	1	1	2	1	1	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?
Montezumia cortesia	1	1	0	0	2	1	1	1	0	1	0	1	0	0	1	1	0	1	0	0	1	0	1	0	1	1	0	1	1	1	1	0	0	0	1	0	0	0	2	1	0	1	0	0	0	0	0	1	0
Montezumia dimidiata	1	1	0	0	2	0	1	1	0	1	1	0	1	0	1	1	0	1	0	2	1	1	1	1	2	1	0	1	1	0	1	0	0	0	0	0	0	0	2	1	0	1	0	0	0	0	0	1	0
Montezumia ferruginea	1	1	0	0	0	1	1	1	0	1	0	0	1	1	1	1	0	1	0	0	1	0	1	0	2	1	0	1	1	0	1	0	0	0	0	0	0	0	2	2	1	1	0	1	0	1	0	0	1
Montezumia ignobiloides	1	1	0	0	1	0	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	2	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	2	1	0	1	0	1	0	0	0
Montezumia infernalis	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1	1	0	0	0	2	0	1	1	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0	1	1
Montezumia liliacea	1	1	0	0	1	1	1	1	0	1	1	0	1	0	1	1	0	1	0	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1
Montezumia morosa	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1	1	0	1	0	2	0	1	1	0	2	1	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
Montezumia nigriceps	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1	1	0	0	1	2	0	1	1	0	2	1	0	1	1	0	1	1	0	1	0	1	0	0	1	0	2	0	1	1	0	0	0	0	1
Montezumia pelagica	1	1	0	0	0	0	0	1	0	1	1	0	1	0	1	1	0	0	0	0	1	1	0	1	0	1	0	1	1	0	1	1	0	1	0	0	0	0	0	1	0	1	0	1	0	0	0	1	1
Montezumia petiolata	1	1	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	2	0	1	1	0	1	2	0	1	1	0	1	1	0	1	0	0	0	0	0	2	2	2	1	1	0	0	0	2	1
Montezumia sparsa	1	1	0	0	1	0	1	1	0	1	1	0	1	1	1	0	0	0	0	0	1	1	1	0	2	1	0	1	1	0	1	1	0	1	0	0	0	0	0	0	2	1	1	1	0	0	0	0	1

FIGURES 5–13. **5–9.** Female head in frontal view: 5. *Mb. apicalipennis*; 6. *Mb. schrottkyi*; 7. *Mt. analis*; 8. *Mt. dimidiata*; 9. *Mt. infernalis*. **10–13.** Female head in dorsal view: 10. *Mb. apicalipennis*; 11. *Mt. dimidiata*; 12. *Mb. funebris*; 13. *Mt. analis*. Scale bars for 5–9 = 2 mm; 10–11 = 1 mm; 12–13 = 0.5 mm.

within both genera. Thus, it is not surprising that this character would consequently be down-weighted in the implied-weighting analyses.

As stated above, *Monobia* is monophyletic provided *Montezumia arizonensis* and *Montezumia aurata* are included in this genus. Bequaert (1940a), when describing *Mt. arizonensis,* commented that this species would be "on the border line of *Monobia* and *Montezumia,* the limits between these genera being arbitrary." Indecision also existed regarding *Montezumia aurata,* which was originally described in *Monobia* by Bertoni (1918) and later transferred to *Montezumia* by Willink (1982). The monophyly of *Monobia* is supported by different homo-plastic transformations when different weighting schemes and values of *k* were used. Under

FIGURES 14–22. **14–15.** Female pronotum in dorsal-oblique view: 14. *Mb. apicalipennis*; 15. *Mt. analis*. **16–18.** Female mesosoma in lateral view: 16. *Mb. apicalipennis*; 17. *Mt. dimidiata*; 18. *Mt. nigriceps*. **19–22.** Female mesosoma in dorsal view: 19. *Mb. apicalipennis*; 20. *Mt. analis*; 21. *Mt. dimidiata*; 22. *Mt. nigriceps*. Scale bars for 14–15 = 1 mm; 16–18 and 22 = 1 mm; 19–21 = 2 mm.

equal weights the evident notauli (char. 20, state 1; fig. 19), the metasomal sternum I more than three times as wide as long (char. 36, state 1; fig. 31), and the absence of carina on the base of the metasomal sternum I (char. 37, state 1; fig. 32) are supportive of the clade. Of special interest is character 37, which does not conform to the condition, cited above, that supports a large clade within *Monobia* (char. 37, state 0; fig. 31). Character 36 (state 1) is maintained as supportive of *Monobia* under implied weighting and *k* values between 3 and 7 in addition of different homoplastic changes (figs. 2 and 3). With implied weighting under *k* values between 8 and 10, characters 20 (state 1) and 37 (state 1) were once again recovered as supportive of the clade (fig. 4).

FIGURES 23–32. **23–24.** Female metanotum in posterior view: 23. *Mt. azurescens*; 24. *Mt. nigriceps*. **25–26.** Female propodeum in posterior view: 25. *Mb. angulosa*; 26. *Mt. azurescens*. **27–28.** Female lower propodeum in lateral view: 27. *Mt. nigriceps*; 28. *Mt. coeruleorufa*. **29–30.** Female tergum I in lateral view: 29. *Mb. quadridens*; 30. *Mt. azurescens*. **31–32.** Female sternum I in ventral view: 31. *Mb. schrottkyi*; 32. *Mt. azurescens*. Scale bars for 23 = 0.3 mm; 24 = 0.5 mm; 25–26, 30–31 = 1 mm; 27–28 = 0.5 mm; 29, 32 = 1 mm.

Within *Monobia, Mt. arizonensis* was always placed as the sister species to the remaining *Monobia,* followed by *Mt. aurata* and *Mb. caridei* Brèthes. The group of *Monobia caridei* was recovered as sister to the group of *Monobia angulosa* de Saussure, which contains the majority of the species within the genus. Species groups proposed for *Monobia* by Willink (1982) were always recovered as monophyla. The group of *Monobia angulosa* is supported by one synapomorphic condition in all analyses: cephalic foveae margined posteriorly by a carina (char. 8, state 0; fig. 12). The internal relationships of the *Monobia angulosa* group varied, with greater resolution reached as *k* values for the implied-weighting scheme were increased (compare figs.
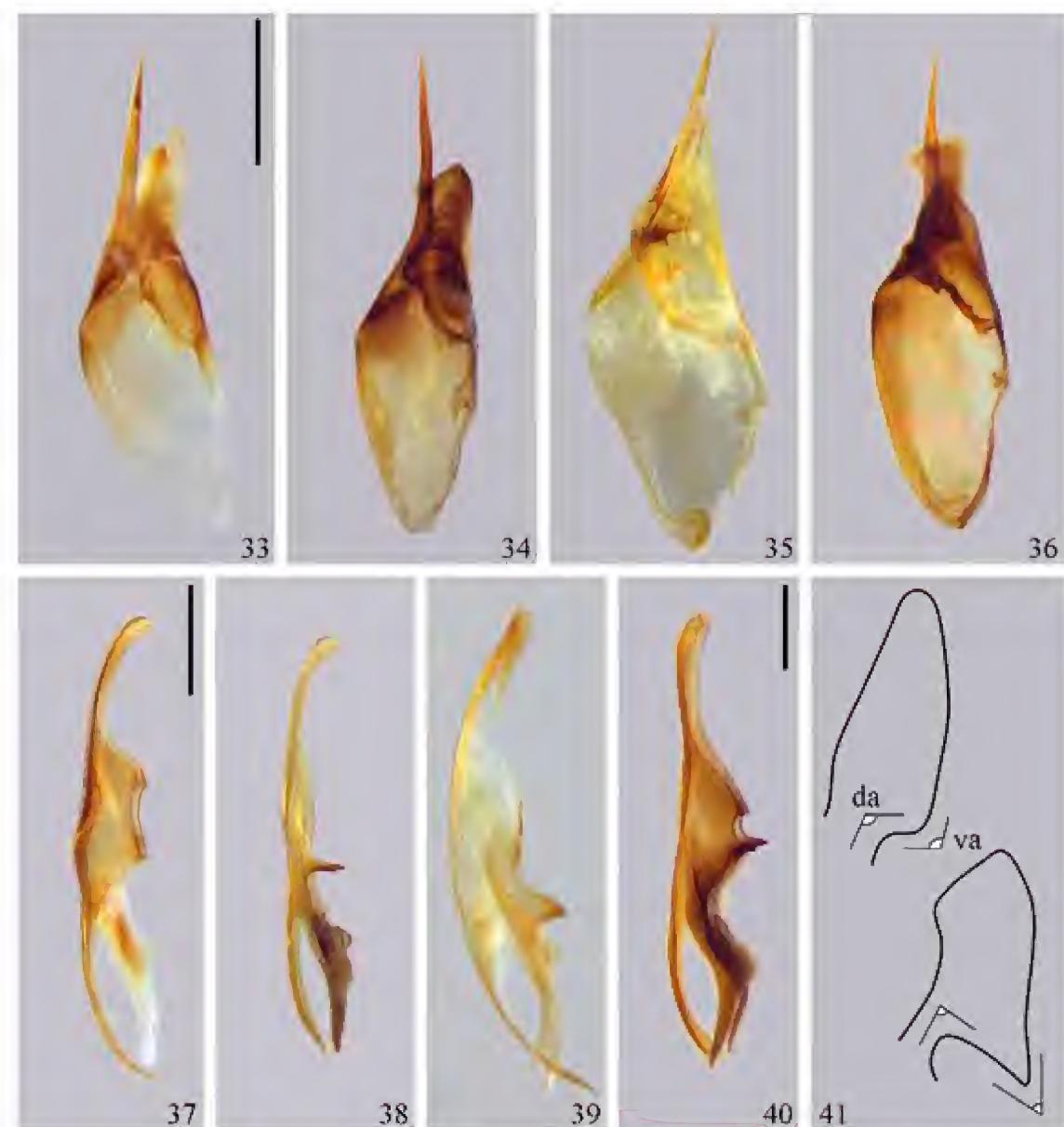
FIGURES 33–41. **33–36.** Male paramere and volsella (digitus and cuspis) in lateral inner view: 33. *Mb. quadridens*; 34. *Mt. analis*; 35. *Mt. azurescens*; 36. *Mt. brethesi*. **37–40.** Male aedeagus in lateral view: 37. *Mb. quadridens*; 38. *Mt. analis*; 39. *Mt. azurescens*; 40. *Mt. brethesi*. **41.** Sketchy representation of the digitus of *Mb. quadridens* and *Mt. analis*: da = basal dorsal angle of digitus; va = basal ventral angle of digitus. Scale bars for 33–35 = 1 mm; figs. 36–39 = 1 mm; 40 = 0.5 mm.

2 and 4), that is, as the weighting function was weakened. Even though topology varied within this group, some relationships were always stable, such as the clade (*Mb. goiana* + *Mb. insueta* + *Mb. triafasciata*), the clade (*Mb. apicalipennis* + (*Mb. funebris* + *Mb. nigripennis*)), and the clade (*Mb. angulosa* + *Mb. cingulata*).

TABLE 5. Branch support values under different methods

Clade	Bremer support values (equal weights)	Resampling (GC values) (equal weights)	Resampling (GC values) (implied weights $k = 3$)
Genus *Monobia*	2	0.36	0.55
Genus *Montezumia*	1	0.32	0.61
Mb. angulosa group	1	0.21	0.66
Mt. azurescens group	1	0.83	0.87
Mt. dimidiata group	3	0.93	0.98
Mt. leprieurii group	3	0.62	0.46
Mt. nigriceps group	1	0.08	0.18

Montezumia is supported by two synapomorphies under equal weights: submarginal carina slightly raised (char. 32, state 1; fig. 27) and preapical longitudinal furrow on metasomal tergum I deep (char. 35, state 1). The raised submarginal carina is present throughout the entire genus, with a different condition (strongly raised: char. 32, state 2; fig. 28) supporting the clade (*Mt. azteca* + (*Mt. azurescens* + *Mt. coerulorufa*)). Despite this character's seeming consistency among species of *Montezumia,* it was not optimized as a synapomorphy for the genus when implied weighting under *k* values between 3 and 7 was applied. Under values between 8 and 10, the condition was once again recovered as a synapomorphy for species of *Montezumia.* This is probably an effect of treating this character as nonadditive multistate.

As observed for the species group of *Monobia angulosa,* internal relationships within *Montezumia* varied when different approaches were considered. Again, greater resolution was obtained when implied weights were applied, increasing even more when higher values of *k* were used (figs. 2 and 3). This trend was maintained to the *k* value of 7, with some branches collapsing when values between 8 and 10 were tested (fig. 4). Among the species group of *Montezumia* proposed by Willink (1982), the group of *Mt. arizonensis* actually belongs to *Monobia.* The group of *Mt. ferruginea* de Saussure contains only one species, but its sister group could not be established from the present results. The group of *Mt. infernalis* (Spinola) was represented in the present study by the species *Mt. aurata* (now placed in *Monobia*), *Mt. ignobi-loides* Willink, *Mt. infernalis,* and *Mt. morosa* de Saussure. It was the only species group not recovered as monophyletic, with its species recovered in different positions in the different analyses. Although sister-group relationships could not be established for the remaining species groups, all groups were corroborated as monophyletic in every tested weighting scheme: the group of *Mt. azurescens* (Spinola) with the topology as (*Mt. azteca* + (*Mt. azurescens* + *Mt. coerulorufa*)), the group of *Mt. leprieurii* (Spinola) with the topology as (*Mt. brethesi* + *Mt. lili-acea* + *Mt. pelagica*), the group of *Mt. nigriceps* (Spinola) with the topology as (*Mt. sparsa* + (*Mt. petiolata* + (*Mt. bruchii* + *Mt. nigriceps*))), and the group of *Mt. dimidiata* de Saussure with the topology (*Mt. analis* + (*Mt. cortesia* + *Mt. dimidiata*)).

Although the values for Bremer branch support were relatively low (fig. 1; table 5), most clades were recovered as monophyletic as indicated above, but their relationships were not always stable. The same is true for branch support using the symmetric resampling method (table 5), with higher support values obtained when the implied weighting was performed (as shown by Goloboff et al., 2008b).

<div align="center">Taxonomy</div>

Monobia and *Montezumia,* as recognized herein, can be readily separated by the submarginal carina raised above the propodeal orifice in the latter, following the key provided by Carpenter and Garcete-Barrett (2003 [2002]). This condition was also recovered as synapomorphic for the species included in *Montezumia* in our analysis (see discussion above).

Three new combinations are proposed for species currently placed in *Montezumia* in congruence with the phylogenetic results: *M. aurata, M. arizonensis,* and *M. oaxaca.* The last species cited was not included in the present analyses, but it is morphologically similar to and included in the group of *Mt. arizonensis,* so its placement follows. Also, a new species of *Monobia* is described. Abbreviations used in the description are: MOW, median ocellus width; POD, minimum distance between posterior ocelli; OED, minimum distance between compound eye and posterior ocellus; and MPOD, minimum distance between median ocellus and a posterior ocellus. For identification purposes, we recommend the use of the keys provided by Willink (1982), as it is still the most comprehensive work on the taxonomy of both *Monobia* and *Montezumia.*

<div align="center">

Monobia arizonensis (Bequaert, 1940), new combination

</div>

Montezumia arizonensis Bequaert, 1940a: 96.
    Type Locality: United States, "Sabino Canyon, Sa. Catalina Mountains, Pima Co. (EUA)."
    Type: Holotype ♀, Cambridge (MCZ).
Montezumia arizonensis: Bohart, 1951: 885. Krombein, 1979: 1498. Rodríguez-Palafox, 1996: 480.

<div align="center">

Monobia aurata Bertoni, 1918, revised combination

</div>

Monobia aurata Bertoni, 1918: 191, 207.
    Type Locality: Paraguay, "Puerto Bertoni."
    Type: Holotype female, depository unknown.
Monobia aurata: Bequaert, 1940b: 826, 830.
Monobia aurata var. *exigua* Bertoni, 1918: 191, 207.
    Type Locality: Paraguay, "Paraguay: Puerto Bertoni."
    Type: Holotype female, depository unknown.
Monobia aurata var. *exigua*: Bequaert, 1940b: 827, 830.
Montezumia aurata: Willink, 1982: 40, 162, 301, 315. Garcete-Barrett, 1999: 8.

<div align="center">

Monobia oaxaca (Willink, 1982), new combination

</div>

Montezumia oaxaca Willink, 1982: 32, 68.
    Type Locality: Mexico, "México, Oaxaca, Guelatao."
    Type: Holotype ♂, Los Angeles (LACM).
Montezumia oaxaca: Rodríguez-Palafox, 1996: 480.

Monobia goiana **Hermes**, new species

Figures 42–47, 53

Diagnosis

Monobia goiana is similar to *M. insueta* Giordani Soika and *M. trifasciata* Willink, running to couplet 8 in Willink's (1982) key, all these species bearing two slight lateral humps on the base of sternum II (fig. 50). *Monobia goiana* is more similar to *M. insueta,* these two differing from *M. trifasciata* by the lack of long erect and pale hairs on head and mesosoma (present in *M. trifasciata*; figs. 42–46, 48, 51–53), narrower gena at the level of eye emargination (broader on *M. trifasciata*; figs. 42, 52), and complete pronotal carina dorsally (interrupted medially on *M. trifasciata*; figs. 44, 51, 53). *Monobia goiana* differs from *M. insueta* by the less evident humeral crest anteriorly (more evident in males of both species), the lack of a differentiated cuticular median area on the mesoscutum (in *M. insueta* the punctures are separated by somewhat raised cuticle devoid of micropunctures; figs. 44, 48), by the dull and weakly punctured surface of terga I–II (shiny and with coarser punctures on *M. insueta*; figs. 47, 49), and by the presence of yellow markings on clypeus, pronotum, tegula, and tergum I of female (absent in *M. insueta*).

FIGURES 42–47. *Monobia goiana*. **42–43.** Habitus: 42. Female; 43. Male. **44.** Female mesosoma in dorsal view. **45–46.** Head in frontal view: 45. Female; 46. Male. **47.** Female metasoma in dorsal view. Scale bars for 42–43 = 3 mm; 44, 47 = 1 mm; 45–46 = 2 mm.

FIGURES 48–53. **48–50.** *Mb. insueta,* female: 48. Pronotum and mesoscutum in dorsal view; 49. Terga I–II in dorsal view; 50. Sterna I–VI in ventral view. **51–52.** *Mb. trifasciata,* female: 51. Head and pronotum in dorsal view; 52. Head and mesosoma in lateral view. **53.** *Mb. goiana,* female head and pronotum in dorsal view. Scale bars for 48–49 = 1 mm; 50, 52 = 2 mm; 51, 53 = 1 mm.

DESCRIPTION

HOLOTYPE: Female.

COLOR: Integument mostly black with yellow markings as follows: band on base of clypeus, mark on lower inner orbit of compound eye, line on dorsal surface of pronotum interrupted medially, most of tegula, obsolete markings on scutellum, small and thin subapical line on tergum I, broad bands on apex of terga II–V, lateral subapical markings on tergum and sternum VI, lateral apical marks on sterna II–V. Foretibiae yellowish chestnut on inner and anterior surfaces. Wing membrane chestnut, venation chestnut becoming brownish at apex. Body covered by short and erect golden hairs, which are longer on head, lateral surface of propodeum, and sterna I–II.

DIMENSIONS: Body from frons to apex of tergum II = 10.0 mm. Forewing length = 9.5 mm. Width of gena equivalent to 0.89 times the width of eye at emargination. Proportion MOW:POD:OED:MPOD equivalent to 1:1.4:1.4:0.5. Dorsal surface of tergum I 2.2 times wider than long.

STRUCTURE: Clypeus flat on center, somewhat depressed on lateral portions, with coarse striatiform punctures on apical two-thirds; clypeal apex concave, with distance between teeth a little smaller than interantennal distance; frons somewhat swollen, with striatiform punctures

intermixed with micropunctures; cuticle around cephalic foveae slightly modified, with foveae delimited posteriorly by an evident and somewhat raised arclike carina; occipital carina strong and sharp, slightly angled on vertex; pronotal carina strong and complete, somewhat lamellar on dorsal surface, interrupted laterally below level of pronotal fovea and then continuous to mesopleural margin; pronotal fovea rounded, broad; dorsal surface of pronotum coarsely striatopunctate; humeral crest sharp especially anteriorly; lateral surface of pronotum depressed with scattered undefined and shallow punctures, reticulate; epicnemial carina strong; mesepisternum coarsely striatopunctate; mesoscutum coarsely striatopunctate, with space between punctures filled with somewhat sparse micropunctation; notauli well marked posteriorly; scutellum strongly punctured, with striatiform punctures restricted to lateral portions, less densely punctured medially where the micropunctures are densely concentrated; lateral crests of metanotum raised; metanotum coarsely striatopunctate, with raised and well-developed transversal crenation along apex of dorsal surface; apex of posterior surface of metanotum devoid of puctures; dorsal surface of propodeum coarsely striatopunctate becoming weaker and scattered on lateral surface; posterolateral angles of propodeum with a strongly pointed projection; posterior surface of propodeum mostly shiny and smooth, with scattered punctures on upper portion and obliquely striate on lower portion, delimited medially by a longitudinal sulcus on upper half and by a sharp carina on lower half; propodeal valvula strongly rounded and continuous with submarginal carina; metasoma with very weak punctures, separated by more than one puncture diameter, reticulate and dull; metasomal sternum II with somewhat stronger punctures than the rest of metasoma; terga I–II broader than long, tergum I with an apical shallow longitudinal furrow; base of sternum II with lateral humps slightly produced.

PARATYPE: Male.

COLOR: As in female, except for extensive yellow markings as follows: clypeus entirely; longitudinal line on scape beneath; broad pronotal band interrupted medially; a spot on upper mesepisternum; broad subapical transversal band on scutellum.

DIMENSIONS: Body from frons to apex of tergum II = 10 mm. Forewing length = 9.1 mm. Width of gena equivalent to 0.9 times the width of eye at emargination. Proportion MOW:POD:OED:MPOD equivalent to 1:1.6:1.6:0.5. Dorsal surface of tergum I 2.5 times wider than long.

STRUCTURE: As in female, except as follows: clypeus with weak and sparse punctation; clypeal apex deeply concave; humeral crest stronger and somewhat lamellar anteriorly; lateral humps on base of sternum II somewhat more developed.

ETYMOLOGY: The specific epithet (feminine) is the demonym applied to the native people of the Brazilian State where the type specimens where collected (Goiás).

SPECIMENS EXAMINED: Holotype: ♀, "Brasil, Goiás, Chapada dos Veadeiros, Fazenda Templo Terra, 14°10′38″S 47°38′33″W, 1220 m, 01.iv.2003, Melo, Aguiar, Marchi e Gonçalves." Paratype: ♂, same data as holotype, except "02.iv.2003." The holotype and the paratype are deposited at Coleção de Entomologia Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná (DZUP), Curitiba, Brazil.

ADDITIONAL SPECIMENS EXAMINED: *Monobia insueta,* 3♂ and 2♀, refs. HYM07926, HYM07927, HYM07928, HYM07929 and HYM07930. *Monobia trifasciata*: 2♂ and 2♀, refs. HYM07996, HYM07999 (Paratype), HYM08003 (Paratype) and HYM08004. These specimens are deposited in the Instituto Miguel Lillo, Tucumán, Argentina.

CONCLUDING REMARKS

Although a number of recent phylogenetic investigations have advanced our understanding of eumenine genera in the Neotropical Region (Willink and Roig-Alsina, 1998; Garcete-Barrett, 2003 [2002]; Hermes and Melo, 2008; Garcete-Barrett and Hermes, 2010; Hermes, 2010), higher-level relationships within the subfamily remain poorly known. Little attention has been paid to this extremely diverse and complex group, yet efforts like the one presented here may be helpful in resolving basic taxonomic problems, such as the placement of species whose generic limits are not clear.

The present study aims to resolve the limits between *Monobia* and *Montezumia* through cladistic analyses. Furthermore, almost all species groups proposed by Willink (1982) are corroborated as monophyletic. Although the monophyly of both genera (taking into account the new combinations proposed) is considered to be well established, as well as the naturalness of most of Willink's species groups, the relationships among most of these groups remain to be discovered. In many cases, it was difficult to translate complex observations into discrete variables, so inclusion of new evidence to the present matrix (e.g., molecular data) would be most welcome.

ACKNOWLEDGMENTS

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